Journal of the Lepidopterists' Society
41(4), 1987, 199–208

HOST SPECIFICITY AND BIOLOGY OF *PROCHOERODES TRUXALIATA* (GUENÉE) (GEOMETRIDAE), A POTENTIAL BIOCONTROL AGENT FOR THE RANGELAND WEED *BACCHARIS HALIMIFOLIA* L. IN AUSTRALIA

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ABSTRACT. *Prochoerodes truxaliata* is an ectophagous foliage feeder native to the western United States. It is multivoltine, with larvae found throughout the year on *Baccharis pilularis*, its only known host. Normal larval development occurred in the laboratory only on species of *Baccharis*, including *B. halimifolia*. Larvae also developed on the closely related *Chrysothamnus nauseosus*, but slow growth and high mortality suggest it is not a natural host. The insect is considered sufficiently stenophagous for introduction into Australia to control *Baccharis halimifolia*.

Additional key words: biological control, *Baccharis sarathroides*, *B. neglecta*.

The woody shrub *Baccharis halimifolia* L. (Asteraceae: Astereae: Baccharineae), an introduction from North America, is a serious weed in Queensland, Australia (Stanley & Ross 1986). The Queensland Department of Lands, through the Alan Fletcher Research Station, has instigated a long-range research program to find biological control agents in the New World for release against this weed in Australia.

One source of potential biocontrol agents is the fauna feeding on species closely related to the weed. Indeed, some authors (Pimentel 1963, Hokkanen & Pimentel 1984) suggest that such insects may be better biocontrol agents because they possess less "ecological homeostasis". Programs against *Opuntia* spp. (Dodd 1929, Fullaway 1954, Pettey 1948) provide examples where insects from hosts other than the target species have given significant control.

Baccharis pilularis is one of 20 United States species of the predominantly South American genus, and is found throughout coastal California and Oregon where two subspecies are recognized. *Baccharis p. pilularis* DC. is a prostrate form found near the coast and often grown as an ornamental. *Baccharis p. consanguinea* DC. is an erect form found further from the coast, and is morphologically very similar to *B. halimifolia*.

Tilden's (1951a) comprehensive survey of the insect fauna associated with *B. pilularis* formed a useful adjunct to the biological control pro-

gram. A number of species listed there were studied further. One, *Rhopalomyia californica* Felt (Diptera: Cecidomyiidae), is already controlling *B. halimifolia* in some areas of Australia (McFadyen 1985). A second, *Trirhabda flavolimbata* (Mannerheim) (Coleoptera: Chrysomelidae), was found to have too wide a host range for introduction; laboratory tests indicated it might breed on *Aster novae-angliae* (Palmer 1985).

A third, *Prochoerodes truxaliata* (Guenée) (Geometridae), is the subject of this paper, which reports studies conducted before permission was sought to introduce the insect for biocontrol purposes. Five of the seven species in the North American genus *Prochoerodes* are general feeders on trees and shrubs. The other two, *P. truxaliata* and *P. amplicineraria* (Pearsall), are so distinct that they may not be congeneric with the others (D. C. Ferguson pers. comm.). *Prochoerodes truxaliata* has been recorded only from *Baccharis pilularis*, although adults have been collected in New Mexico, Utah, Colorado, and Arizona, all outside the range of *B. pilularis*. One specimen of *Prochoerodes amplicineraria* has been reared from *Chrysothamnus nauseosus*.

Botanical nomenclature here follows Bailey and Bailey (1976) or Correll and Johnston (1979).

Biology

Moths (illustrated in Holland 1968) were nocturnal, emerging from resting places at dusk. They were observed hovering above *Baccharis pilularis* as late as 0100 h at Davis, California. Copulation occurred in early evening and oviposition commenced about three days after eclosion. Unmated females produced sterile eggs. One mated female laid 231 eggs, and after death contained a further 119 undeveloped eggs, for a total brood of 350. Females oviposited on the plant, but as the eggs have little exochorion they usually fell to the ground. Females also oviposited as they crawled on the ground around the plant.

Eggs were pale green, nearly spherical (0.8 mm diam.), smooth and glossy, but fertile eggs turned brown within 48 h. Eclosion occurred in 8 to 10 days at room temperature (26°C).

Larvae left eggs by eating a hole in the chorion without eating the shell, doubled their size by inhaling air, and exhibited negative geotropism by climbing any available object. The following nondiagnostic larval description is given only for special field use. First instars were dark gray with pale lateral vittae. The head was straw colored with numerous small dark dots, the absence of which from the frons gave the appearance of a frontal line. Thoracic legs and prolegs were also straw colored. Second instars were a translucent neutral gray with faint

dark lateral stripes, and lacked the disproportionately large head of the first instar. Third and later instars were brown, which intensified with maturity. Mature larvae were irregularly dotted with dull black, the dots coalescing to form poorly defined dorsal and lateral stripes. Subdorsal pale lines bordered the dorsal stripe, and two irregular light lines extended laterally, forming a margin to the lateral stripe. The first thoracic and abdominal spiracles were orange, often with blue centers. A pair of short fleshy protuberances was present on the fourth abdominal tergite, and there were indications of a second pair of protuberances on the fifth segment. Abdominal setae were black. In the laboratory, mean development times for 7 instars (N = 8) reared on *B. pilularis* were 4, 4, 5, 6, 7, 11 and 12 days, respectively. Two of 10 individuals underwent an 8th instar.

Small larvae created "windows" in leaves but larger larvae consumed foliage from the leaf edge backwards, often consuming the whole leaf. Most larval growth and foliage consumption occurred in the last two instars. Fully grown larvae were 40–45 mm long. Larvae remained on the foliage during the day, but most feeding occurred at night. Resting larvae assumed a typical geometrid posture. Small larvae, when disturbed, dropped and returned on silk strands attached to the plant. Large larvae clung tightly to twigs and were difficult to dislodge. Mature larvae ceased feeding about three days before pupation and sometimes wandered away from the foliage.

Pupation occurred in a slight cocoon made either in the foliage or on the ground. If on the plant, larvae gathered several leaves together with a few strands of silk to form the cocoon. Pupae were obtect, and 15–20 mm long. Larvae were reared on clusters of *Baccharis neglecta* foliage to compare growth of the sexes. Male pupae were lighter (mean 0.21 ± SE 0.04 g, N = 90) than female pupae (0.32 ± 0.07 g, N = 50). Development times from egg to adult averaged 66.2 ± 0.5 (N = 90) and 70.0 ± 0.6 (N = 50) days for males and females, respectively, at 26°C.

There were three generations a year at Davis and Stanford, California, but larvae were present throughout the year, and overwintered in this stage. Large larvae were present at the end of winter, and produced moths in early April. A second generation was seen in mid-summer, and an autumn generation produced moths in October.

Larvae were collected from both subspecies of *B. pilularis*, but infrequently and then usually at low densities (one or two per bush). Very high densities (hundreds per large bush) were occasionally found near Davis, and these severely defoliated plants. The insect has occasionally become a pest of ornamental *B. p. pilularis*.

REARING

A laboratory colony was started and maintained for a number of generations using the following procedure. Wild moths were collected and confined in paper cups for oviposition. Resultant neonate larvae were transferred to clusters of foliage (*Baccharis pilularis, B. halimifolia,* or *B. neglecta*) held in a 37 × 27 × 17 cm plastic shoe box. Approximately 20 larvae were placed on each cluster. They were transferred to fresh foliage twice a week.

Pupae were collected from the container bottom and foliage, and placed with sugar-water wicks and branches of *Baccharis* in a plastic shoe box with the bottom replaced by fly mesh. Eggs fell through the fly mesh, and were collected from paper towelling under the cage. Eggs were refrigerated for about a month without ill effect; moths, larvae, and pupae could also be cooled for at least a week.

HOST SPECIFICITY

Host specificity of *P. truxaliata* was determined by examining pinned specimens in major entomological collections, and conducting laboratory trials to determine oviposition preference, neonate feeding, feeding behavior of late instars, and behavior in a multiple choice situation.

Museum records. Collections at the University of California (Berkeley, Davis, and Riverside); California Academy of Science, San Francisco; Los Angeles County Museum of Natural History; National Museum of Natural History, Washington, D.C.; and American Museum of Natural History, New York, were examined. Most specimens in these collections had been taken at light traps. Limited data on pinned specimens nominated *B. pilularis* as host.

Oviposition preference. Cages approximately 1 m^3 were placed in a temperature-controlled glasshouse. Cages contained four potted plants, each of a different species, and each resting in a 30-cm diam. white dish in a cage corner. Sixteen laboratory-reared pupae (6 female, 10 male) were placed in a cup at cage center with sugar-water wicks. After eclosion and oviposition, eggs in the white dishes were counted. The plants were further tended and examined every alternate day, and any larvae present on the foliage were counted. Each cage of four plant species was replicated twice. Egg numbers were analyzed by analysis of variance (using a log N + 1 transformation) to determine differences in ovipositional preference. Four such series using different plant species were studied and separately analyzed.

Prochoerodes truxaliata exhibited an ovipositional preference for some species over others, with *Baccharis halimifolia* being a preferred host (Table 1). Larvae were found only on *B. halimifolia* and *Chryso-*

TABLE 1. Numbers of eggs collected from dishes surrounding potted plants after oviposition, and numbers of larvae observed on plants. Each series replicated twice.

	Mean no. eggs	Mean maximum no. larvae
Series 1		
Baccharis halimifolia L. (Tribe Astereae)	50 a*	25
Chrysothamnus nauseosus (Pall.) Britt. (Astereae)	49 a	20
Aster novae-angliae L. (Astereae)	0 b	0
Bellis perennis L. (Astereae)	2 b	0
Series 2		
B. halimifolia	89 a*	20
Solidago altissima L. (Astereae)	40 a	0
Conyza canadensis (L.) Cronq. (Astereae)	19 a	0
Lactuca sativa L. (Lactuceae)	120 a	0
Series 3		
B. halimifolia	268 a*	3
Chrysanthemum morifolium Ramat. (Anthemidae)	89 a	0
Tagetes lucida Cav. (Tageteae)	89 a	0
Cynara scolymus L. (Cardueae)	39 a	0
Series 4		
B. halimifolia	189 a*	13
A. novae-angliae	18 b	0
Dahlia pinnata Cav. (Heliantheae)	3 b	0
Gaillardia pulchella Foug. (Heliantheae)	4 b	0

* Means separated by different letters differ significantly (<0.05) by the LSD test from other means in the same series.

thamnus nauseosus. Those on the former developed normally to pupation, but those on the latter developed much more slowly and with a very high mortality in later instars, only one larva successfully pupating and producing a normal looking moth.

No-choice feeding of neonate larvae. Five unfed, neonate, laboratory reared larvae were placed in a paper cup with a young leaf of one plant species. Leaves were changed daily and after 72 h survival was assessed. Not all plants could be tested at the one time but *Baccharis halimifolia* was always included as a control with each series. Each treatment was replicated at least three times and, where possible, foliage was obtained from different plants for replication.

Results (Table 2) show that larvae survived only on *B. halimifolia*, *B. neglecta*, *B. pilularis*, *B. sarathroides*, and *Chrysothamnus nauseosus*, and on these species survival was approximately 80%. Larvae did not survive on *Baccharis glutinosa*, *B. bigalovii*, *B. pteronioides*, or on 22 other plant species.

Feeding by later instars. The ability of late instars to develop on three plant species was evaluated. Larvae 20 mm long and approximately 14 days old were selected from a colony raised on *B. neglecta*

TABLE 2. Survival of neonate larvae after 72 h exposure to leaves of various plant species.

Plant	No. replications	Mean percentage survival
Tribe Astereae		
Baccharis halimifolia	12	80
B. neglecta Britt.	12	79
B. pilularis DC.	6	96
B. sarathroides Gray	3	80
B. glutinosa Pers.	6	0
B. bigelovii Gray	3	0
B. pteronioides (DC.) Gray	3	0
Chrysothamnus nauseosus	3	92
Isocoma wrightii (Gray) Rydb.	6	0
Gutierrezia microcephala (DC.) Gray	3	0
Aster novae-angliae	3	0
Conyza canadensis	3	0
Solidago altissima	3	0
Tribe Anthemideae		
Leucanthemum maximum (Raymond) DC.	3	0
Chrysanthemum morifolium	3	0
Artemisia tridentata Nutt.	3	0
Tribe Heliantheae		
Xanthium strumarium L.	3	0
Parthenium hysterophorus L.	3	0
Helianthus annuus L.	3	0
Gaillardia pulchella Foug.	3	0
Zinnia elegans Jacq.	3	0
Dahlia pinnata Cav.	3	0
Tribe Inuleae		
Antennaria fallax Greene	3	0
Tribe Eupatoreae		
Eupatorium compositifolium Walt.	3	0
Tribe Lactuceae		
Lactuca sativa L.	3	0
Other families		
Vicia faba L. (Fabaceae)	3	0
Lycopersicon esculentum L. (Solanaceae)	3	0
Cucurbita pepo L. (Cucurbitaceae)	3	0
Albizia julibrissan Durazz. (Mimoaceae)	3	0
Delonix regia (Bojer) Raf. (Caesalpiniaceae)	3	0

foliage. Five larvae were placed on foliage clusters of *B. halimifolia*, *Chrysothamnus nauseosus* (closely related to *Baccharis*, and on which neonate larvae were able to feed) and *Aster novae-angliae* L. (more distantly related to *Baccharis*, and on which neonates had not been able to feed). At intervals of 2 or 3 days for 14 days, larval lengths were

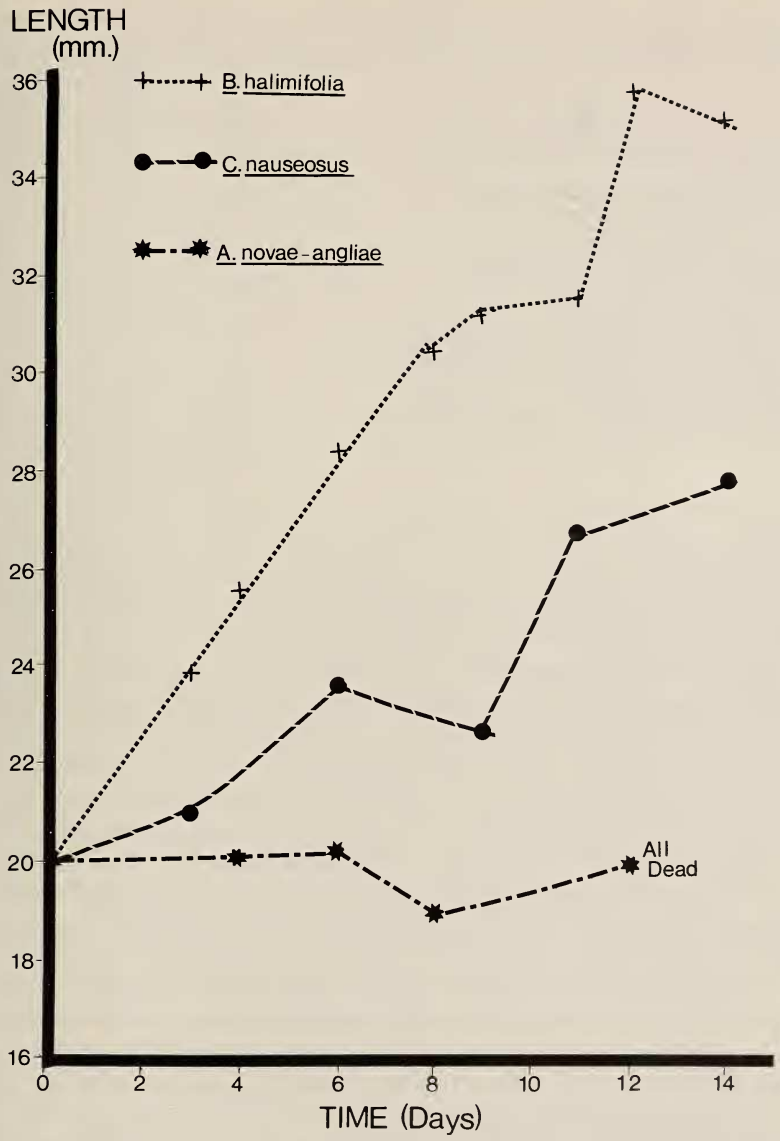

FIG. 1. Growth in length of larvae on *Baccharis halimifolia*, *Chrysothamnus nauseosus*, and *Aster novae-angliae*. Points represent means for 5 larvae.

measured—a simple procedure because larvae naturally assume a stick-like posture on the leaves.

Three distinctively different growth rates resulted (Fig. 1). While larvae survived for up to 12 days on *Aster novae-angliae*, fed somewhat

TABLE 3. Indices of preference in a multiple-choice experiment with two replications.

Plant	Mean distribution index	Mean percentage foliage consumed	Mean no. leaves nibbled
Baccharis halimifolia (Tribe Astereae)	66	25	27
B. neglecta	13	33	19
Gutierrezia microcephala (Astereae)	2	<1	3
Isocoma wrightii (Astereae)	18	<1	7
Aster novae-angliae (Astereae)	0	0	0
Xanthium strumarium (Heliantheae)	<1	0	0
Dahlia pinnata (Heliantheae)	<1	0	0
Zinnia elegans (Heliantheae)	<1	0	0
Leucanthemum maximum (Anthemideae)	0	0	0
Chrysanthemum morifolium (Anthemideae)	0	0	0
Tagetes lucida (Tageteae)	0	0	0
Gerbera jamesonni Bolus ex Hook (Mutisieae)	1	0	0

on the foliage and produced frass, negligible growth occurred, and after the first few days the larvae looked unhealthy. Those on *Chrysothamnus nauseosus* displayed an intermediate growth rate.

Multiple-choice experiment. A multiple-choice experiment was conducted to determine whether larvae responded similarly on whole plants and cut foliage, and to observe their response when given a choice of plant species. A 53 × 69 × 84 cm cage covered with fly mesh was set up to contain 12 potted plants, each of a different species. Wooden planks were placed above the pots so that foliage and stems protruded through small holes in the planks which acted as a floor and facilitated larval movement between plants. Some hundreds of unfed neonate larvae and eggs were scattered over this floor, simulating the natural distribution of eggs on the ground around plants. The plants were examined daily for the duration of larval development, and the larvae on each plant counted. A distribution index (Palmer 1985) indicating relative larval abundance on each plant was calculated. Number of leaves attacked and an estimate of total feeding were recorded for each plant at the end of the experiment.

Results (Table 3) indicated that *Baccharis* was the preferred host. Few larvae were seen on the non-*Baccharis* plants, and most of them were found in the first few days. None of the other species proved suitable, although some feeding was evident on the closely related *Isocoma wrightii* and *Gutierrezia microcephala*. Toward the end of the experiment, some of the *Baccharis* were considerably defoliated but there was no movement of the large larvae to other plants.

DISCUSSION

Host specificity testing indicated that this insect is highly stenophagous, and that its host range is restricted to *Baccharis* species. Four *Baccharis* species appeared to be equally suitable hosts. This result suggests that *B. sarathroides* may be the host in Arizona, New Mexico, Colorado, and Utah where moths have been collected but *B. pilularis* is not found. A degree of affinity between *Prochoerodes truxaliata* and *Chrysothamnus nauseosus* was also evident, and reflects the phylogenetic relation between *Baccharis* and other North American genera within tribe Astereae. This result, and the host range of another California insect, *Aristotelia argentifera* Busck (Gelechiidae), which is reported only from *B. pilularis* and *Ericameria ericoides* (Lessing) (Tilden 1951b), support the hypothesis of B. J. Turner (pers. comm.) that *Chrysothamnus* and *Ericameria* are the most closely related genera in North America to *Baccharis*.

The insect seems sufficiently stenophagous for biological control use in Australia. It was also tested against a further 6 species in tribe Astereae and another 15 species in other tribes of Asteraceae including most of the commercially important ones. This degree of testing closely related species is greater than commonly done for potential biocontrol agents (Diatloff & Palmer 1987). The partial affinity with *Chrysothamnus nauseosus* is not important in the Australian context because this genus, like most North American genera of the tribe, is not found in Australia. *Conyza canadensis*, *Solidago altissima* and *Aster novae-angliae* are North American species introduced into Australia, and are probably the most closely related of the present Australian flora to *Baccharis*. As such, they might serve as the "critical test species" advocated by Wapshere (1975). Clearly, these plants were not suitable for *Prochoerodes truxaliata*. However, before final clearance for release in Australia, some testing against native species of Tribe Astereae should be undertaken there.

Prochoerodes truxaliata might also be utilized as a biological control agent within the United States. In Texas, *Baccharis neglecta* and *B. salicina*, extremely closely related and often confused (Correll & Johnston 1979), are considered weedy, and have recently been recognized as a management problem on grazing lands (Scifres 1980). It might therefore be possible to introduce the insect into Texas to control these species. It is considered safe for introduction there (R. Bovey pers. comm.).

Although ectophagous Lepidoptera have not been associated with many successful biological control programs, *Prochoerodes truxaliata* does have many desirable features of a good biocontrol agent. It is

multivoltine, highly fecund, capable of causing considerable damage to the host plant, and easily reared in the laboratory. Also, it does not have a strong diapause, a factor which might be particularly useful in Australia where winters are mild. There would appear to be good prospects of this moth establishing on *Baccharis halimifolia* if introduced for biological control.

ACKNOWLEDGMENTS

We thank L. E. Ehler, University of California, Davis, for help over the years; D. C. Ferguson for expert identification and helpful advice concerning *Prochoerodes* taxonomy; and B. L. Turner, University of Texas, Austin, for advice on phylogenetic relations of *Baccharis* to other genera.

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Received for publication 3 April 1987; accepted 9 September 1987.